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Genetic structure and admixture in sheep from terminal breeds in the United States

K. M. Davenport*, C. Hiemke†, S. D. McKay‡, J. W. Thorne*,§, R. M. Lewis¶, T. Taylor and B. M. Murdoch***

*Department of Animal and Veterinary Science, University of Idaho, Moscow, ID 83844, USA. †Niman Ranch and Mapleton Mynd Shropshires, Stoughton, MA 53589, USA. ‡Department of Animal and Veterinary Sciences, University of Vermont, Burlington, VT 05405, USA. §Texas A&M AgriLife Extension, San Angelo, TX 76901, USA. ¶Department of Animal Science, University of Nebraska–Lincoln, Lincoln, NE 68583, USA. **Department of Animal Science, Arlington Research Station, University of Wisconsin–Madison, Arlington, WI 53911, USA.

Summary

Selection for performance in diverse production settings has resulted in variation across sheep breeds worldwide. Although sheep are an important species to the United States, the current genetic relationship among many terminal sire breeds is not well characterized. Suffolk, Hampshire, Shropshire and Oxford (terminal) and Rambouillet (dual purpose) sheep ($n = 248$) sampled from different flocks were genotyped using the Applied Biosystems Axiom Ovine Genotyping Array (50K), and additional Shropshire sheep ($n = 26$) using the Illumina Ovine SNP50 BeadChip. Relationships were investigated by calculating observed heterozygosity, inbreeding coefficients, eigenvalues, pairwise Wright's F_{ST} estimates and an identity by state matrix. The mean observed heterozygosity for each breed ranged from 0.30 to 0.35 and was consistent with data reported in other US and Australian sheep. Suffolk from two different regions of the United States (Midwest and West) clustered separately in eigenvalue plots and the rectangular cladogram. Further, divergence was detected between Suffolk from different regions with Wright's F_{ST} estimate. Shropshire animals showed the greatest divergence from other terminal breeds in this study. Admixture between breeds was examined using ADMIXTURE, and based on cross-validation estimates, the best fit number of populations (clusters) was $K = 6$. The greatest admixture was observed within Hampshire, Suffolk, and Shropshire breeds. When plotting eigenvalues, US terminal breeds clustered separately in comparison with sheep from other locations of the world. Understanding the genetic relationships between terminal sire breeds in sheep will inform us about the potential applicability of markers derived in one breed to other breeds based on relatedness.

Keywords genetic admixture, genetic relationships, sheep, terminal sheep breeds

Introduction

The production of lamb and wool is an important agricultural industry in the United States, with approximately 5 million sheep and 80 000 operations (USDA ERS 2019). According to the American Sheep Industry National Animal Health Monitoring System's most recent study, 81.6% of operations raise sheep for meat purposes (American Sheep Industry 2011). The most popular breeds used for meat production include the Suffolk, Hampshire, Shropshire, Oxford, and Southdown (American Sheep Industry 2011). To make progress in their own flocks, some US lamb and wool producers have implemented quantitative genetic selection strategies using estimated breeding values through the National Sheep Improvement Program (NSIP) to identify and select animals with desirable traits (Wilson & Morrical 1991; Notter 1998; Lupton 2008). As this program is more widely utilized, the improvement of product quality and yield of lamb and wool products in the United States is anticipated to accelerate.

Previous research indicates that selection for various traits such as wool or growth within breeds of sheep has led to greater breed specialization across the world (Kijas *et al.* 2012; Zhang *et al.* 2013). However, many breeds of sheep have retained greater heterozygosity in comparison with other species, including cattle (Bovine HapMap Consortium

Address for correspondence

B. M. Murdoch, Department of Animal and Veterinary Science, University of Idaho, Moscow, ID 83844, USA.
E-mail: bmurdoch@uidaho.edu

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et al. 2009; Kijas *et al.* 2012). Furthermore, sheep from similar locations have been reported to have high levels of admixture (Blackburn *et al.* 2011; Kijas *et al.* 2012).

The current genetic structure and level of admixture among terminal sire breeds in the United States have not been well characterized (Zhang *et al.* 2013). The objective of this study was to examine population structure and admixture in sheep from terminal breeds from US sheep operations in collaboration with producers engaged with NSIP. Understanding the genetic relationships between terminal sire breeds in the United States will allow us to better understand the genetic relatedness of these breeds of sheep and assess the potential applicability of information based on breed relatedness. Further, this study can help elucidate how biological differences segregate in different breeds, as well as between breeds of sheep.

Materials and methods

Sample collection and DNA isolation

A total of 248 sheep from terminal breeds of sheep including Hampshire ($n = 45$ from six flocks), Suffolk ($n = 68$ from nine flocks in the Midwest and $n = 37$ from one flock, the University of Idaho Suffolk flock, in the West), Oxford ($n = 11$ from two flocks) and Shropshire ($n = 44$ from five flocks), as well as wool/dual-purpose Rambouillet ($n = 43$ from one flock), were genotyped for this study. Blood, semen or tissue samples were collected by individual producers and shipped to the University of Idaho and DNA was isolated using the phenol chloroform method previously described (Sambrook *et al.* 1989).

Genotyping and quality control

Samples were genotyped using the Applied Biosystems™ Axiom™ Ovine Genotyping Array (50K) consisting of 51 572 SNPs (Thermo Fisher Scientific, catalog number 550898). A subset of Shropshire samples ($n = 26$) previously genotyped on the Ovine Illumina SNP50 Bead Chip consisting of 54 241 SNPs (Illumina catalog number WG-420-1001) was also included in this dataset. The genotypic data for these samples, from each platform, were merged by SNP name and location in PLINK version 1.90, with a total of 47 485 SNPs overlapping between the two panels. Quality control of genotype data was performed using PLINK version 1.90 specifically excluding SNPs with a call rate of less than 0.90 and MAF less than 0.01, resulting in 45 864 SNPs remaining in the analyses (Purcell *et al.* 2007; Chang *et al.* 2015).

Observed heterozygosity, inbreeding coefficients, and F_{ST} calculations

The observed heterozygosity was estimated for each animal using PLINK version 1.90 and averaged by breed (Purcell *et al.* 2007; Chang *et al.* 2015). Inbreeding coefficients were calculated for each animal based on the observed and expected homozygosity in PLINK version 1.90, and the mean and 95% confidence intervals were calculated with the R package 'rcompanion' in R version 3.6.1. To remove redundancy and provide a more accurate representation of variation, LD pruning was performed using the --indep-pairwise function in PLINK version 1.90 with an $r^2 = 0.5$, a sliding window size of 50 SNPs and shifts of five SNPs (Visser *et al.* 2016; Gilbert *et al.* 2017). After LD pruning, 40 121 SNPs remained for further analyses. Pairwise F_{ST} was estimated in PLINK version 1.90 between breeds of sheep using the LD pruned dataset (Purcell *et al.* 2007; Chang *et al.* 2015).

Eigenvalue analyses

Eigenvalues were calculated using the filtered SNP dataset for terminal breeds only and then with Rambouillet in SNP and Variation Suite version 8.7.2 (Golden Helix, Inc., www.goldenhelix.com). The top two eigenvalues were plotted against each other in SNP and Variation Suite.

Hierarchical clustering

An identity by state matrix was calculated from the LD pruned dataset pairwise between all sheep using the PLINK version 1.90 --distance flag (Purcell *et al.* 2007; Chang *et al.* 2015). The matrix was read into R version 3.6.1 and hierarchical clustering based on the identity by state matrix of Hamming distances between each animal using the 'hclust' function. The Bioconductor package 'ctc' was used in R version 3.6.1 to write a Newick file to import into DENDROSCOPE 3 software (Huson & Scornavacca 2012). A rectangular cladogram was drawn from the Newick file in DENDROSCOPE version 3.5.9 (Huson & Scornavacca 2012). Individual branch labels were colored according to producer-reported breed of sheep.

Admixture analysis

The program ADMIXTURE version 1.3.0 was implemented to examine admixture between all samples using the LD pruned genotypes in BED format (Alexander *et al.* 2009; Decker *et al.* 2014). The most probable number of *K* given populations was estimated using the lowest cross-validation error (Alexander *et al.* 2009; Akanno *et al.* 2018). Euclidean distances were calculated in R version 3.6.1 with the *adegenet* package and an analysis of molecular variance (AMOVA) was performed with the *pegas* package with 1000 permutations to statistically examine differences between populations (McKay *et al.* 2008; Paradis 2010; Jombart & Ahmed 2011).

International breed comparisons

Genotypes from 2819 sheep from 74 breeds across the world were retrieved from the International Sheep Genome

Consortium Sheep HapMap Database and used in comparison with US terminal breeds including the addition of $n = 5$ Dorset and $n = 7$ Southdown sheep from the United States. The same set of 45 864 SNPs used with the US terminal breeds was then merged with the same SNPs from the Sheep HapMap dataset. Eigenvalues were calculated between US terminal breeds and the same breeds from other locations in the HapMap dataset, all US breeds in this study and the same breeds present from other locations in the HapMap dataset, and all US breeds in this study and the Sheep HapMap dataset.

Results

Observed heterozygosity and inbreeding coefficient

To examine the relatedness of animals within each of the breeds, observed heterozygosity and average inbreeding coefficient were calculated. These statistics were calculated based on observed and expected homozygosity, estimated for each individual, and averaged for each breed (Table 1). The Oxford animals exhibited the greatest (0.35) observed heterozygosity and lowest inbreeding coefficients. Similar observed heterozygosity was exhibited by Shropshire (0.34), Western Suffolk (0.34), Suffolk (0.33) and Hampshire (0.33). Shropshire had the lowest inbreeding coefficient (0.09) in comparison with the Suffolk (0.13), Western Suffolk (0.14) and Hampshire (0.14). The group with the lowest observed heterozygosity (0.30) and highest inbreeding coefficient (0.16) was Rambouillet.

Wright's F_{ST}

Wright's F_{ST} was calculated pairwise between each group of animals to examine differentiation between breeds (Table 2; Wright 1965; Weir & Cockerham 1984; Lenstra *et al.* 2012). In general, values between 0 and 0.05 are categorized as 'little to no differentiation,' values between 0.05 and 0.15 as 'moderate differentiation', values between 0.15 and 0.25 as 'great differentiation', and values above 0.25 as 'very great differentiation' between populations tested (Weir & Cockerham 1984; Frankham *et al.* 2002). Rambouillet is considered greatly differentiated from all terminal breeds. Interestingly, Western Suffolk are considered moderately differentiated from other terminal breeds. Little to no difference was detected between Hampshire and Suffolk or Hampshire and Shropshire. Furthermore, although Western Suffolk and other Suffolk are not reported as different breeds, they too exhibit moderate differentiation.

Eigenvalue analyses

To investigate how individuals from reported terminal breeds the US group or cluster, eigenvalues were calculated and plotted for all samples (Fig. 1). An eigenvalue plot for only terminal breeds of sheep (Fig. 1a) as well as terminal breeds and Rambouillet sheep (Fig. 1b) is displayed. In Fig. 1a, the largest difference of eigenvalues is between Western Suffolk and Shropshire and can be observed on the *x*-axis of the plot shown. Further, the animals sampled for the Shropshire breed exhibited the largest spread of eigenvalue points. Interestingly, all Suffolk did not group together. Most of the Suffolk animals sampled cluster closely with Hampshire animals; however, the Western Suffolk flock clustered separately from Hampshire and other Suffolk animals.

In Fig. 1b, Rambouillet animals cluster together, and the entire breed clusters distinctly and away from the terminal sheep breeds on the largest eigenvalue axis. Similar to Fig. 1a, sheep cluster primarily by breed with the exception of four Shropshire animals. The Suffolk samples do not all group together, with Western Suffolk clustering separately from other Suffolk animals. With these notable exceptions, animals within a breed cluster together.

Hierarchical clustering based on identity by state

To examine how animals from breeds of sheep in the United States are related to those from other breeds, hierarchical

Table 1 The mean observed heterozygosity and average estimated inbreeding coefficient including the 95% confidence interval for each group.

Breed	Observed heterozygosity	Inbreeding coefficient[1]	95% Confidence interval for inbreeding coefficient
Hampshire	0.33	0.14	0.12–0.15
Suffolk	0.33	0.13	0.12–0.15
Western Suffolk	0.34	0.14	0.13–0.15
Oxford	0.35	0.05	0.01–0.09
Shropshire	0.34	0.09	0.04–0.11
Rambouillet	0.30	0.16	0.15–0.17

[1]Inbreeding coefficients are reported as Fhat2 and calculated by: (observed heterozygosity − expected)/(total − expected).

Table 2 Pairwise F_{ST}[1] between breeds of sheep.

	Hampshire	Suffolk	Western Suffolk	Oxford	Shropshire
Hampshire	0				
Suffolk	0.03	0			
Western Suffolk	0.09	0.07	0		
Oxford	0.06	0.06	0.13	0	
Shropshire	0.05	0.06	0.11	0.06	0
Rambouillet	0.17	0.17	0.23	0.18	0.16

[1]Wright's F_{ST} values between 0 and 0.05 are categorized as no differentiation, 0.06–0.15 as moderate differentiation, 0.16–0.25 as great differentiation, and >0.26 as very great differentiation.

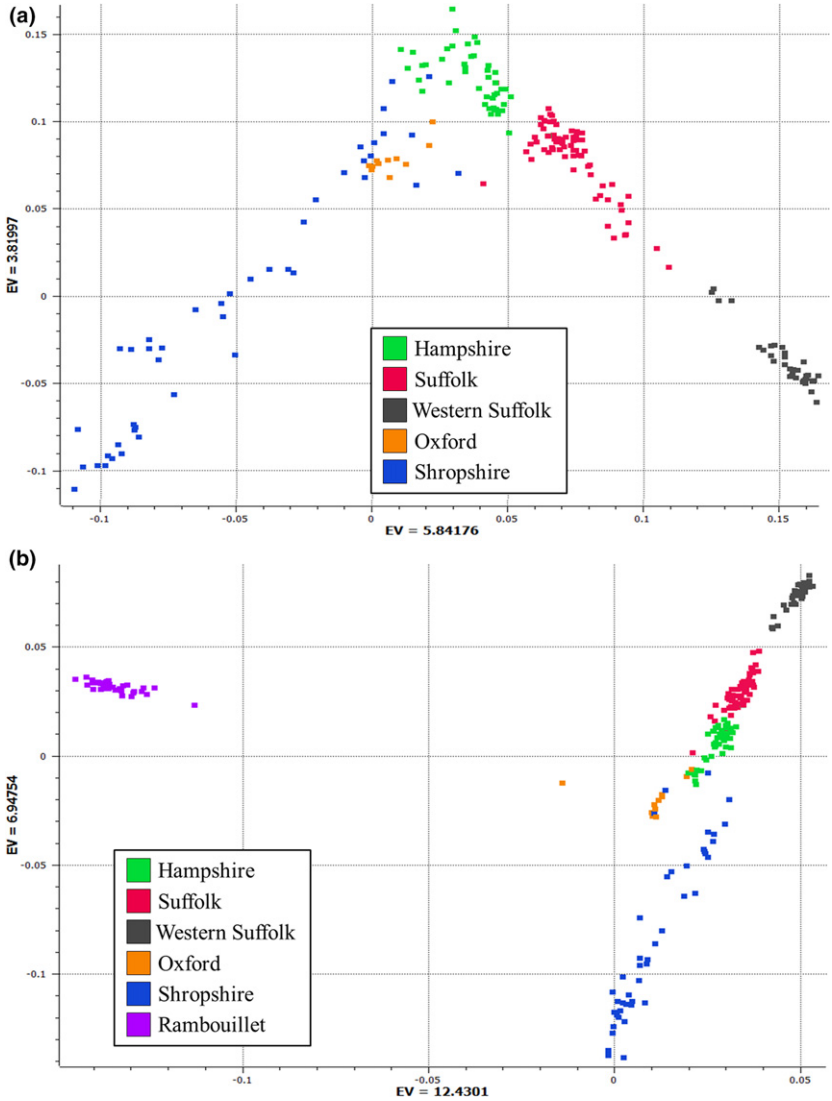

Figure 1 Plot of calculated eigenvalues for breeds of US sheep. (a) Eigenvalues plotted for US terminal breeds of sheep. (b) Eigenvalues plotted for US terminal breeds and Rambouillet sheep. Each point represents an individual animal and points are colored by reported breed.

clustering was performed using an identity by state matrix. A rectangular cladogram was constructed to visualize the hierarchical clustering (Fig. 2). All Western Suffolk, Oxford and Rambouillet animals clustered together by breed. Rambouillet animals clustered in a distinct, separate branch from all other breeds, which was consistent with the eigenvalue plot. In general, most sheep were more identical by state to other animals within the same breed with a few notable exceptions.

Several reported Shropshire animals clustered with the Hampshire branches; these were the same animals that clustered with the Hampshire breed in the eigenvalue plots. A branch of Shropshire animals also clustered closely with a larger branch of Hampshire sheep. Additionally, Suffolk and Hampshire animals overlapped and appeared to cluster closely within the branches of the cladogram. Still, overall most breeds clustered independently with the few exceptions mentioned before.

Admixture analysis

An admixture analysis was performed using the program ADMIXTURE to investigate the extent of admixture between different breeds of sheep in this study (Alexander *et al.* 2009; Decker *et al.* 2014; Getachew *et al.* 2017). The analysis was conducted using two to 10 given populations. The best fit of K given populations was determined as $K = 6$ based on the cross-validation values calculated in ADMIXTURE (Fig. S1; Akanno *et al.* 2018). Further, the AMOVA analyses showed significant ($P < 0.01$) differences between the $K = 6$ assigned populations.

In the best fit $K = 6$ plot, admixture was detected within terminal breeds (Fig. 3). Admixture between terminal breeds was observed in Hampshire, Oxford, Suffolk and Shropshire, but the Western Suffolk population showed little admixture with other terminal breeds except Suffolk. Not surprisingly, the dual-purpose Rambouillet sheep were different from the US terminal breeds examined.

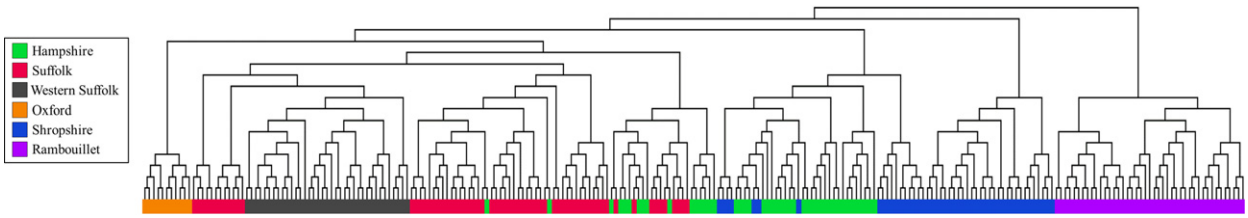

Figure 2 Rectangular cladogram of individuals clustered based on identity by state and colored by reported breed.

Eigenvalue plots of US and international comparisons

To examine how US sheep compare with other sheep across the world, genotyping data from this study were merged with data from the Sheep HapMap (Kijas *et al.* 2012; Kijas 2013). Eigenvalues were calculated and plotted with US terminal breeds including additional Dorset and Southdown sheep from the United States, and animals of the same breeds from the Sheep HapMap dataset (Fig. 4a). Interestingly, the US terminal breeds clustered closer to other breeds from the United States than the same reported breed, including Suffolk and Dorset, from other locations. When the genetic information for wool breeds of sheep was included, they clustered apart from the terminal breeds (Fig. 4b). Figure 4b also shows the Irish Suffolk clustering closely with Suffolk from the United States. Finally, when all samples were considered, the US terminal breeds clustered with similar breeds from Australia and the UK (Fig. 4c). In summary, animals clustered closest with those of similar geographic location in the eigenvalue plots.

Discussion

The observed heterozygosity results from this study were consistent with data reported in other breeds of sheep across the world (Kijas *et al.* 2012; Ciani *et al.* 2014; Gaouar *et al.* 2017). More specifically, the observed heterozygosity in most breeds was close to what was reported in Australian sheep (Kijas *et al.* 2012; Al-Mamun *et al.* 2015). In addition, the observed heterozygosity was consistent with other US sheep including Suffolk, Rambouillet, Columbia, Polypay and Targhee (Zhang *et al.* 2013). However, the breeds in this study had lower observed heterozygosity when compared with Boutsko, Karagouniko and Chios breeds from Greece (Michailidou *et al.* 2018).

In our study, Oxford sheep exhibited the lowest average inbreeding coefficient and highest observed heterozygosity, similar to Finnsheep (Li *et al.* 2011). This is probably because these sheep were selected based on pedigree diversity from NSIP, whereas Western Suffolk had one of the highest inbreeding coefficients and was only represented by one flock. However, to our surprise, the inbreeding coefficient for Western Suffolk was similar to that of Suffolk, which included animals from 10 separate flocks. Perhaps this is because these animals are the result of and representative of the breeding strategies of purebred flocks. Other work in 97 sheep breeds across the world including Ethiopian sheep reported inbreeding coefficients between −0.07 and 0.16 and observed heterozygosity between 0.061 and 0.343, which are similar to our results (Edea *et al.* 2017; Zhang *et al.* 2018).

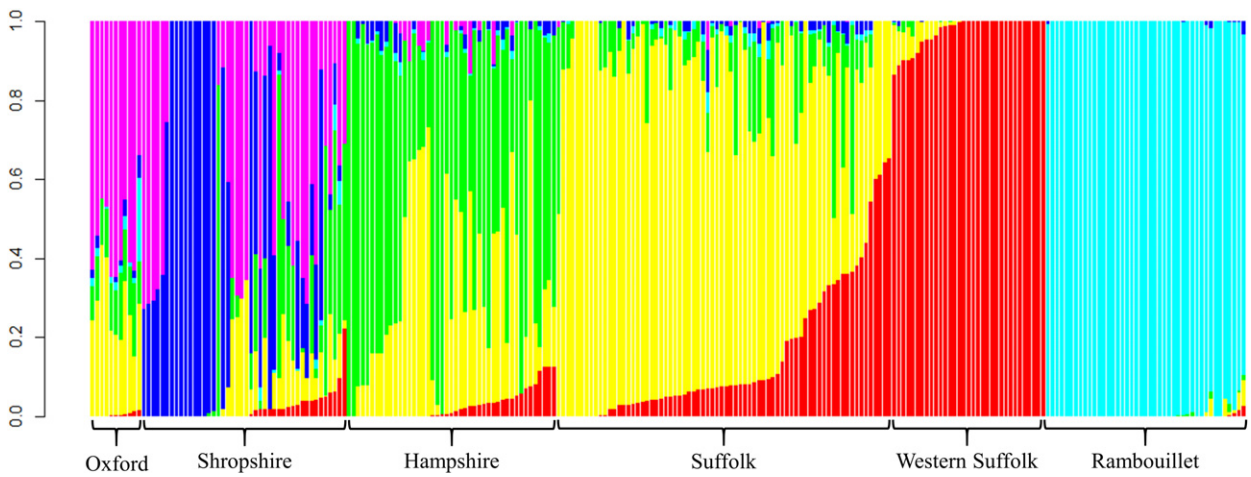

Figure 3 ADMIXTURE model clustering output with $K = 6$ populations. Each bar represents an individual animal for each terminal breed and Rambouillet, and the six colors represent each K population cluster.

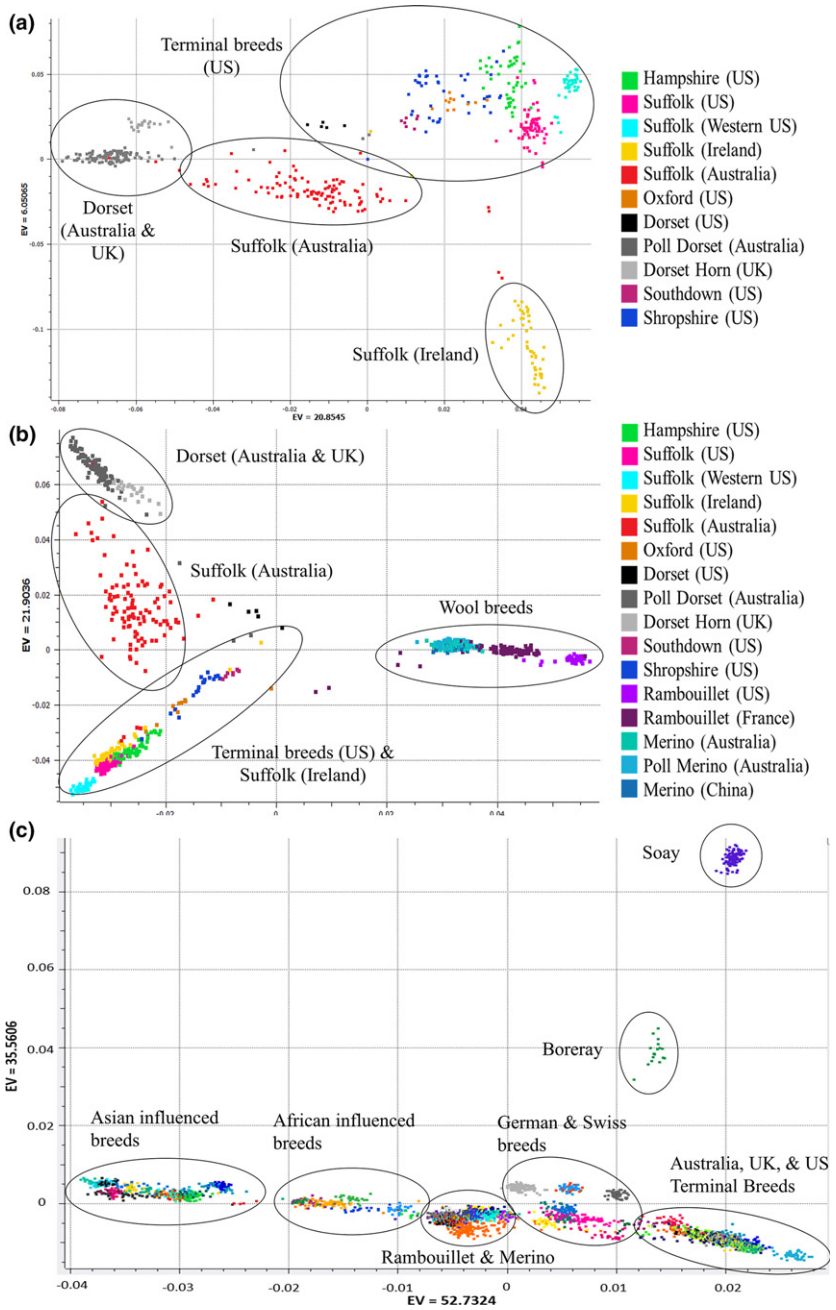

Figure 4 Eigenvalue plots of US sheep in this study compared with other breeds across the world as part of the Sheep HapMap study. (a) Eigenvalue plot of US terminal breeds and Dorset and Suffolk HapMap breeds. (b) Eigenvalue plot of all US sheep in this study compared with HapMap terminal and wool sheep. (c) Eigenvalue plot of US sheep in this study compared with all breeds present in the Sheep HapMap study.

Despite similarity in inbreeding coefficient and heterozygosity estimates, Western Suffolk shows moderate differentiation from Suffolk whereas Hampshire, Oxford, Shropshire and Suffolk show little to moderate differentiation from each other. The Western Suffolk consists of representatives from a 'closed flock', which may explain the divergence from the more broadly sampled Suffolk. The lack of differentiation observed between the Suffolk, Hampshire and Shropshire is not surprising considering the prevalence of crossbreeding in many US terminal breed flocks. It is worth noting that the Southdown is thought to be a common ancestor for Hampshire, Shropshire and Oxford breeds (Ryder 1964). These points are strongly supported by the results of the ADMIXTURE analysis. Furthermore, these results concur with previous research that reported a Wright's $F_{ST} = 0.1621$ between Suffolk and Rambouillet; these breeds differ in origin as the Rambouillet breed was derived from Merino bloodlines (Dickinson & Lush 1933; Zhang *et al.* 2013).

Differences between breed groups can be visualized in the eigenvalue plots, where sheep cluster primarily by reported breed with the exception of a few animals. The separation of Suffolk from Western Suffolk is apparent, which is consistent with previous work that identified regional differences in Suffolk from the United States (Kuehn *et al.* 2008). The

Shropshire breed has a large spread of eigenvalues and a few animals cluster with Oxford and Hampshire, suggesting the occurrence of crossbreeding. The distinct clustering of the Rambouillet away from other breeds clearly displays the genetic difference between terminal and wool/dual-purpose breeds in the United States.

The $K = 6$ plot, supported by the AMOVA analysis, shows that sheep cluster primarily by breed with some level of admixture between all terminal breeds, with the exception of Western Suffolk, which exhibits little admixture except with other Suffolk. The observed admixture within Hampshire, Suffolk, Oxford and Shropshire is potentially due to the use of sires with composite influence from other breeds in US commercial operations (Ercanbrack & Knight ; Norberg & Sørensen 2007). Rambouillet sheep showed little to no admixture with the US terminal breeds examined in this study.

When US sheep were compared with other populations across the world, sheep primarily clustered closest to other animals in similar geographic locations rather than to the same reported breeds in other parts of the world (Kijas *et al.* 2012). More specifically, Suffolk and Dorset animals clustered closer to other US groups than to Suffolk from Australia and Ireland, or Dorset from Australia or the UK. This observation may be partially attributed to the differences in selection and breeding strategies and in production systems across the world (Andersson 2012; Ćurković *et al.* 2016; Wang *et al.* 2015). In addition, the difference between terminal breeds and wool breeds is clear, suggesting that there are genetic differences between breeds that have been selected for alternative production objectives and purposes (Blackburn *et al.* 2011; Zhang *et al.* 2013; Fariello *et al.* 2014).

In summary, we characterized relationships between sheep from terminal sire breed populations in the United States. Internationally, there has been an increased emphasis on genetic selection of sheep for a variety of traits and purposes. Marker-assisted selection is growing in popularity as new technology is being rapidly developed, along with an increase in the use of quantitative genetic programs that calculate estimated breeding values. By better understanding the population structure and admixture between terminal breeds in the United States compared with breeds across the world, we can improve the effectiveness of this developing technology. Our research provides insight into the current relatedness of the popular terminal breeds in the United States and the framework for future analyses on a larger scale.

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Data availability

Data (50K SNP) have been deposited in Open Science Framework (https://osf.io/d7s59/?view_only=9c85566d0ac542d89a62150524eaad0e).

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1 ADMIXTURE cross-validation output plotted across *K* populations.